ALTERING LIFE HISTORY TRAITS: A SIZE-SELECTIVE PREDATOR DECREASES THE SIZE OF ITS PREY

THESIS

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By

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Abstract

Predators negatively influence prey primarily through decreasing their total abundance. However, size-selective predators may also decrease fecundity through selective removal of large, more fecund individuals. To determine how size-selective predators affect life history traits of their prey, we examined size at first reproduction, maximum size, and neonate size of the zooplankter *Bosmina* as a function of saugeye (walleye, *Sander vitreus*, females x sauger, *S. canadense*, males) density in fish hatchery ponds. We hypothesized that prey size would decrease with increased predation according to the size-efficiency hypothesis. From linear regression analyses we found marginally significantly smaller size at first reproduction (SFR) and smaller maximum size (MAX) with increased predation. We found marginally smaller neonate size (NEO) with increased predation. Due to the marginal explanatory power of predation, additional factors (bottom-up, maternal, and time effects) were examined. Ponds were fertilized with either 20 or 30 $\mu g\ L^{-1}$ of phosphorus allowing us to look at the bottom-up effect. From a one-way ANOVA, we found significantly larger SFR and a marginally significantly larger MAX in the 30 $\mu g\ L^{-1}$ of phosphorus ponds. We used a multivariate analysis to examine simultaneously the effects of predation and fertilization. The results showed that sizes decreased at the same rate with increased predation independent of the fertilization rate. Additionally, from linear regression, we found that maternal effects played a significant role in determining *Bosmina* NEO and MAX. Finally, we found that SFR significantly decreased while MAX significantly increased temporally during the production season. These results indicated that this system has multiple factors that contribute to altering *Bosmina* life history traits and that the removal of large individuals

may lead to decreased trophic efficiency by decreasing the energy reaching higher trophic levels, which will lead to less fish production in a hatchery.

Introduction

The relationship between predator and prey may be exceptionally influential to the surrounding biotic community. This "consumer controlled" (top-down effect) could alter the prey population in various ways. A large number of predators could reduce biodiversity of the prey community or result in a decrease in the density of the prey population. Predators have been known to strongly impact the zooplankton community by acting as a selective force influencing the evolution of defense strategies in the prey (Hellsten et al. 1999). Predator-prey relationships have been studied numerous times using different organisms, with different results (Brooks and Dodson 1965, Lampert 1993, Declerck and Weber 2003). The importance of fish predation has been evaluated relative to the structure of zooplankton communities (e.g., Mills et al. 1987), but few studies have investigated the importance of zooplankton size in fish production. The information collected on zooplankton size and how predators alter it could provide helpful cues to a successful predator-prey abundance ratio and consequently, successful fish production in a hatchery setting (Mills et al. 1987).

Fish are known to be size-selective predators (Brooks and Dodson 1965, Mayer and Wahl 1997, Declerck and Weber 2003, Gliwicz et al. 2004). Zooplanktivorous fish prey selectively on conspicuous zooplankton, selecting large, pigmented, and/or actively moving individuals (Brooks and Dodson 1965, Ślusarczyk 1997). Fish predation varies seasonally, having a great effect on zooplankton size through the spring to the summer

period (Kerfoot 1974, Stenson 1976, Culver 1980, Lampert 1993). This variation in the predator community can cause zooplankton life history traits to be phenotypically altered in response to the presence or absence of a predator (Ślusarczyk 1997, Vos et al. 2002, Pangle et al. 2007). This alteration, although costly, may be advantageous to the zooplankton population when high predation exists (Declerck and Weber 2003). Larger zooplankton individuals are suppressed during high predation and small-bodied zooplankton are favored or benefit from the presence of fish (Brooks and Dodson 1965, Ślusarczyk 1997, Vos et al. 2002). Although size-selective predation may cause the majority of the zooplankton population to be small in size, it allows the zooplankton community to persist despite predation.

Predator-prey studies usually focus on the change in abundance of prey due to predation (Mills et al. 1987, Spencer et al. 1999 Gliwicz et al. 2004, Nagata et al. 2005). However, Ślusarczyk (1997) found that *Bosmina*'s size distribution was strongly affected by a size-selective predator. The purpose of our experiment was to investigate how the presence of a size-selective predator affects the size distribution of the zooplankton community. We proposed three predation-related hypotheses based on the Size-Efficiency Hypothesis (Brooks and Dodson 1965):

> *Hypothesis 1*. As fish predation increases, zooplankter size at first reproduction (SFR) will decrease. Zooplankters are more visible to their predators if they are carrying eggs and, therefore, maturing at a smaller SFR may increase the chance of survival and reproduction.

Hypothesis 2. As fish predation increases, zooplankter maximum size (MAX) will decrease. When fish are present, smaller zooplankers will prevail because fish are size-selective predators. Therefore, zooplankton population MAX will decline when predators are abundant. Also, an earlier maturing population will lead to a smaller zooplankter MAX.

Hypothesis 3. As fish predation increases, zooplankter neonate size (NEO) will decrease. Reduced NEO may simply be a physiological consequence of a reduced SFR as NEO commonly depends on adult female size (Kerfoot 1974, Arts and Sprules 1988, Lampert 1993, Vos et al. 2002). Doksæter and Vijverberg (2001) observed both a reduced SFR and a smaller NEO in *D. hyaline x galeata* with fish predation.

Further, we proposed and tested a fourth hypothesis examining the relative importance of top-down versus bottom-up (e.g., fertilization) effects:

Hypothesis 4. The top-down, consumer-controlled effect will be more important or have a stronger influence than the bottom-up, nutrient limitation-controlled effect in this particular ecosystem due to the high density of fish stocked in each pond.

We tested these hypotheses by determining three life history traits in *Bosmina* sp.: (1) size at first reproduction, (2) maximum size, and (3) neonate size and examining how

they varied against an index of pond-specific predation and as a function of pond-specific fertilization regimen. Further, we examined the role of other factors, such as maternal and/or temporal effects.

Methods

We originally sought to use the water flea *Daphnia* sp. as the zooplankton prey due to the long record of studies on the life history of this genus, but due to the high preference for this genus by the zooplanktivorous fish (young-of-year saugeye, *Sander vitreus* females *x S. canadense* males) stocked into the aquaculture ponds, density of this species were low and we therefore studied life history variation as a function of predation and fertilization rates in the smaller cladoceran *Bosmina* sp.

Field sampling

Zooplankton samples were collected from 12 ponds at the Hebron State Fish Hatchery located in southern Licking County, Ohio, in 2003. The ponds were all stocked at a density = 50 saugeye m^{-3}, but through time the ponds experienced different rates of fish mortality, resulting in different levels of predation at the end of the experiment. A predation index (# of saugeye returned m^{-3} in each pond) was calculated to estimate predator density. All hatchery ponds were fertilized to maintain water concentrations of either 20 or 30 $\mu g\ L^{-1}$ of phosphorus (P). Consequently, both top-down (predation) and bottom-up (productivity) effects are possible in a particular pond.

Bosmina was usually sampled twice a week, from 12 April through 19 May 2003, using a 0.5-m diameter zooplankton net (64-μm mesh). Zooplankton samples were

preserved with sugared formalin and stored in The Ohio State University's Limnology Laboratory.

Laboratory sample processing

The first 100 *Bosmina* individuals encountered in a sample were measured (with a Wild Heerbrug dissecting microscope at 50x magnification) from the top of the head to the base of the spine (Culver 1980, Tollrian 1995) with the lengths and number of eggs (if any) recorded. All raw ocular micrometer length measurements were converted to mm using an established conversion factor (1 ocular unit = 0.0183 mm). If fewer than 10 ovigerous females were encountered in the first 100 individuals, additional subsamples were examined. All calculations of SFR, MAX, and NEO followed Culver (1980) and are given in the following equations:

SFR = the 10^{th} percentile length of ovigerous females,

MAX = the 95^{th} percentile length of all females, and

NEO = the 5^{th} percentile length of non-ovigerous females.

Testing the relationship between life history traits and predation and fertilization rates

A simple linear regression of life history size versus predation index was used to test for predation effects. We hypothesized a negative correlation between SFR, MAX, and NEO versus predation index if size-selective predation affected prey size.

An analysis of covariance (ANCOVA) was used to test simultaneously for the effects of fertilization and predation. We hypothesized that sizes would decrease more quickly in 20 μg P L^{-1} ponds than 30 μg P L^{-1} ponds.

An analysis of variance (ANOVA) was used to determine whether there was a significant bottom-up, nutrient effect. Data for SFR and MAX were separated into 20 and 30 μg P L^{-1} groups to determine whether 30 μg P L^{-1} ponds had individuals with a larger SFR or MAX.

A simple linear regression was used to test whether maternal size (SFR) influenced NEO or MAX. We hypothesized that individuals from a population with a smaller SFR would have small NEO and MAX, if mothers' size was an important predictor of NEO and MAX.

Using an ANOVA, we also examined the importance of time through the aquaculture season. We first separated the SFR and MAX data into early and late dates. The first three dates in the data set were used for the "early" times and the last three dates in the data set were used for the "late" times. We hypothesized that through time, SFR and MAX would decrease due to juvenile fish's selection for larger zooplankton.

Results

Top-down, predation effect

SFR marginally significantly decreased ($P = 0.058$, $R^2 = 3.3\%$; Fig. 1A) as predation index increased whereas MAX significantly decreased ($P = 0.006$, $R^2 = 6.8\%$; Fig. 1B) and NEO marginally significantly decreased ($P = 0.088$, $R^2 = 2.7\%$; Fig. 1C). However, very little variation was explained by any of the regression relationships (Fig.

1). Due to the marginally significant results for NEO, it was not examined for bottom-up or time effect.

Both SFR and MAX were larger in the 30 μg P L^{-1} ponds even when the predation index was the same (Figs. 1A-B). SFR reached a greater size in the 30 μg P L^{-1} ponds even when the predation index was high. The SFR decreased further in the 20 μg P L^{-1} ponds. MAX in both the 20 and 30 μg P L^{-1} reached a high size of around 0.40 mm with exception of one 30 μg P L^{-1} pond, which had a maximum size of 0.43 mm. MAX for *Bosmina* appeared to decrease further in 20 μg P L^{-1} ponds than in 30 μg P L^{-1} ponds.

Bottom-up, nutrient effect

When we examined the bottom-up effect for SFR and MAX, we found that SFR increased with increasing P loading (one-way ANOVA, $F_{1,108} = 4.66$, $P = 0.033$; Fig. 2A). This was statistically significant, but is unknown if it is biologically significant because the size difference between the 20 μg P L^{-1} and the 30 μg P L^{-1} ponds was < 0.04 mm. Similarly, MAX increased with increased P loading (one-way ANOVA, $F_{1,108} = 3.84$, $P = 0.053$; Fig. 2B). Although these results are statistically significant it is unknown if they are biologically significant because the size difference was only 0.04 mm.

Simultaneously comparing the importance of predation and fertilization on SFR (Table 1) and MAX (Table 2), we found that these sizes decreased at similar rates independent of fertilization rate.

Maternal effect

NEO significantly increased with SFR ($P < 0.001$, $R^2 = 48.4\%$; Fig. 2A) suggesting that females with larger SFR produce larger neonates. However, the pond with the largest SFR, 0.37 mm, did not exhibit the largest NEO possibly due to high predation (47.1 m^{-3}). Similarly, MAX increased with increased SFR ($P < 0.001$, $R^2 = 22.6\%$; Fig. 2B). These results supported our hypothesis with the largest SFR, 0.37 mm, having the largest MAX, 0.43 mm and were also from a 30 μg P L^{-1} pond.

Time effect

To determine whether life history traits varied through time, data were divided into early and late time periods. Sampling was done during the months of April and May, thus early time became April's three earliest dates and late time became May's three latest dates. We found that SFR significantly decreased through time (one-way ANOVA, $F_{1,108} = 44.86$, $P < 0.001$; Fig. 3A) and MAX increased through time (one-way ANOVA, $F_{1,108} = 4.72$, $P = 0.034$; Fig 3B)

Discussion

Bosmina SFR decreased marginally with increased predation, but this decrease was not as dramatic as our first hypothesis predicted. In the presence of a visual predator, planktonic animals grow more slowly (Pangle et al. 2007). *Bosmina* allocates more energy to reproduction than to somatic growth with increased predators, which enables them to mature earlier at a smaller size, and produce more eggs (Ślusarczyk 1997). Therefore, a female with a smaller SFR may have a greater chance of survival and reproduction than a female maturing at a larger SFR.

Size-selective predation may lead to a change in clonal composition of the population. Previous studies have shown that differences in life history traits between clones is the main reason for specific clone survival when predators are present (Culver 1980, Arts and Sprules 1988, Ebert 1991, Tessier and Consolatti 1991, Glazier 1992, Tessier et al. 1992, Lampert 1993). Clones with a low SFR are favored with predation.

SFR may also respond phenotypically in the presence of a predator. This idea of a phenotypic response under variable predation pressure was discussed in Weider and Pijanowska (1993). These two mechanisms of altering life history do not have to be looked at as separate hypotheses, but may be combined. Our findings support those of Lampert (1993), who stated that selective predation favors clones with a more effective phenotypic response; therefore, SFR may be enhanced by a genotype-by-environment interaction.

Supporting our second hypothesis was the decrease in MAX with an increase in predation. Lampert (1993) examined the correlation between SFR and NEO, so we decided to extend analysis of the maternal effect and we found a tight correlation between SFR and MAX. Maturing at a smaller size will lead to a smaller maximum size, which is a beneficial tradeoff in the presence of a size-selective predator.

The results of NEO versus predation were contrary to our expectations, because NEO did not decrease steadily with predation, but decreased until a minimum size threshold was met (0.18 mm). Neonates can decrease in size, but only to a certain point until they reach the smallest possible size for a neonate. As predation increased, NEO decreased from a maximum size of 0.22 mm to a common minimum of 0.18 mm. Therefore, neonates are still affected by predation. Due to predation, SFR and MAX were

affected and as a result, affected the NEO. The more intense the predation is, the smaller the SFR, leading to a smaller NEO.

Another factor that positively contributed to size was increased P loading. The extra phosphorus allowed for more productivity and, consequently, larger zooplankter size, similar to the findings of Tew et al. (2006). Higher phosphorus loading facilitated the persistence of the *Bosmina* population. Since there still was a decrease in zooplankton size with an increase in phosphorus, it is possible for predation (top-down effect) to be the dominating effect in these pond systems. The negative relationship between planktivores and zooplankton found in this study supports the "cascading trophic interaction" hypothesis (Brooks and Dodson 1965, Carpenter et al. 1985, Galbraith 1967, Hall et al. 1970, Hutchinson 1971, Stenson 1972, O'Brien and de Noyelles 1974, Anderson et al. 1978, McQueen et al. 1986). However, the results also showed that phosphorus is important for stimulating continued zooplankton production, even in these highly nutrient-rich systems.

Time also played an important role in this experiment. Predation increased through the duration of the sampling period. Our results for decreased SFR were congruent with our hypothesis. Although predation index was greatest at the early dates, larval fish may have been too small to consume larger *Bosmina* due to gape-limitation (Nagata et al. 2005). Arumugam and Geddes (1987) found that fish growth, mouth gape and daily food consumption all show exponential increases with time; therefore the impact of larval fish on zooplankton would be insignificant at the early stages, but would become marked at later stages (Arumugam and Geddes 1996). As a result, predation did

not have a huge impact on *Bosmina*'s early SFR. This may have triggered *Bosmina* to mature and reproduce early, resulting in a smaller SFR later in the season.

The results we found for MAX were not what we hypothesized. Instead of decreasing through time, MAX increased through time. This result cannot be easily explained. One hypothesis about this result may be due to environmental factors. Although this was statistically significant, the graph shows an increase in maximum size from early to late dates. Fig. 4A shows a decrease in SFR, but with more favorable environmental factors (e.g., temperature) later in the season, *Bosmina* with a smaller SFR may have been able to have the same or larger MAX as individuals earlier in the season.

According to Persson (1987) the attack of perch decreases with decreasing cladoceran size, but also decreases with increasing fish size for perch $\geq$ 100mm (Persson et al 1996). Since fish are still present in the system, *Bosmina* is still reproducing at a smaller size, while fish may have switched to feeding on benthic macroinvertebrates or even cannibalism. This switch in food preference for the fish may only be present in last date sampled, but may have a large enough effect to increase MAX in the "late" category.

This experiment is a valid model of a trophic cascade that can be applied to lake and hatchery systems. If there is a large top-down effect in a lake, there will be a decline in zooplankton abundance and size. With larger cladocerans absent in the system, zooplankton cannot reduce the phytoplankton biomass (McQueen et al. 1986). This will then lead to an abundance of phytoplankton and possibly algal blooms. The resulting blooms would likely discourage tourists from visiting certain aquatic vacation sites. In an area that relies on tourist dollars for financial stability, the resulting lack of visitors could have an economic impact on the area.

However, this study was directly associated with fish production in an aquaculture setting and was broadly designed to examine predator-prey interactions in order to facilitate maximum fish production. Many assume there is a predation threshold in these ponds, so ponds can be stocked with a certain amount of fish before they completely deplete their food source (zooplankton). If the predation index exceeds the threshold, fish will switch to benthic invertebrates (e.g., chronomids and ostracods), which are less nutritious than zooplankters, causing the fish to be malnourished and possibly smaller, or they will switch to cannibalism, decreasing final yields. In this study, we found that the number of fish stocked in each pond did not affect greatly the SFR and MAX, and the zooplankton community, consequently, was able to survive and reproduce. The addition of phosphorus helped counteract these levels of predation, but the level of fertilization must be carefully monitored. If exceeded, an abundance of phytoplankton may cause low dissolved oxygen, a condition that is directly lethal to fish (Tew et al. 2006). In an aquaculture setting, optimizing the number of fish that can be stocked before a drastic zooplankton community decline would be extremely beneficial.

To improve or build on the results from this experiment, various future projects could be performed. Increasing the sample size, to > 100 individuals would result in more accurate measurements of SFR, MAX, and NEO. Stocking ponds with a greater abundance of fish could better identify the threshold for a predation effect. This may also contribute to a more abrupt decline in zooplankter size and further support the experimental hypotheses. Zooplankter egg number and size was not examined, but future work on these parameters could be used to determine how a size-selective predator affects these life history traits. We would expect, in the presence of a predator, *Bosmina*

with a smaller SFR would have many small eggs, maximizing the chance of one of their offspring surviving. A quantitative analysis of egg-bearing individuals could be done comparing high- and low-predation ponds. Ślusarczyk (1997) compared egg-bearing females between fish and fish-free enclosures and found that large, egg-carrying individuals were absent in the presence of fish, which would also be expected for high predation ponds. Further, synthesizing fish diets with an analysis such as that performed here would help quantify changes in consumptive demand through time. We expect that fish would eat larger zooplankters and zooplankters with eggs, but we were unable to examine this directly in this experiment.

We demonstrated that a size-selective predator altered the SFR and MAX of its prey. However, this is not a simple system where all changes in prey life history traits result from a single factor. To better understand this system, multiple other factors (bottom-up, maternal, and time effects) were investigated and either showed a positive of negative effect on the zooplankton population. This should be taken into consideration when conducting future experiments.

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Literature Cited

Arts, M.T. and W.G. Sprules. 1988. Evidence for indirect effects of fish predation on maternal lipid movement in *Holopedium gibberum*. Canadian Journal of Fisheries and Aquatic Sciences **45**:2147-2155.

Arumugam, P.T. and M.C. Geddes. 1987. Feeding and growth of golden perch larvae and fry (*Macquaria ambigua* Richardson). Transactions of the Royal Society of South Australia, Inc. **111**:59-65.

Arumugam, P.T. and M.C. Geddes. 1996. Effects of golden perch (*Macquaria ambigua* (Richardson)) larvae, fry and fingerlings on zooplankton communites in larval-rearing ponds" an enclosure study. Marine and Freshwater Research **47**:847-844.

Brooks, J. L., S. I. Dodson. 1965. Predation, body size, and composition of plankton. Science **150**:28-35.

Carpenter, S.R., J.K. Kitchell, and J.R. Hodgson. 1985. Cascading trophic interactions and lake productivity. BioScience **35**:634-639.

Culver, D.A., 1980. Seasonal variation in the sizes at birth and at first reproduction in Cladocera. Pages 358-3666 in W.C. Kerfoot, editor. Evolution and ecology of zooplankton communities. Unversity press of New England, Hanover, New Hampshire, USA.

Declerck, S. and A. Weber. 2003. Genetic differention in life history between *Daphnia galeata* populations: an adaptation to local predation regimes? Journal of Plankton Research **25**:93-102.

Doksæter, A. and J. Vijverberg. 2001. The effects of food and temperature regimes on life-history responses to fish kairmones in *Daphnia hyalina* x *galeata.* Hydrobiologia **442**:207-214.

Ebert, D. 1991. The effect of size at birth, maturation threshold and genetic differences on the life-history of *Daphnia magna.* Oecologia **86**:243-250.

Galbraith, M.G. 1967. Size selective predation of *Daphnia* by rainbow trout and yellow perch. TransPhysical Scienceactions of the American Fisheries Society **96:**1-10.

Glazier, D.S. 1992. Effects of food, genotype, and maternal size and age on offspring investment in *Daphnia magna*. Ecology **73**:910-926.

Gliwicz, Z.M., A. Jawiński, and M. Pawlowicz. 2004. Cladoceran densities, day-to-day variability in food selection by smelt, and the birth-rate-compensation hypothesis. Hydrobiologia **526**:171-186.

Hall, D.J., W.E. Cooper, and E.E. Werner. 1970. An experimental approach to the production dynamics and structure of freshwater animal communities. Limnology and Oceanography **15**:839-929.

Hellsten, M., R. Lagergren, and J. Stenson. 1999. Can extreme morphology in *Bosmina* reduce predation risk from L*eptodora*? An experimental test. Oecologia **118**:23-28.

Hutchinson, B.P. 1971. The effect of fish predation on the zooplankton of ten Adirondack lakes with particular reference to the alewife *Alosa pseudoharengus*. Transactions of the American Fisheries Society **100**:325-335.

Kerfoot, W.C. 1974. Egg-size cycle of a cladoceran. Ecology **55**:1259-1270.

Lampert, W. 1993. Phenotypic plasticity of the size at first reproduction in Daphnia: the importance of maternal size. Ecology **74**:1455-1466.

Mayer, C.M. and D.H. Wahl. 1997. The relationship between prey selectivity and growth and survival in a larval fish. Canadian Journal of Fisheries and Aquatic Science **54**:1504-1512.

McQueen, D.J., J.R. Post., and E.L. Mills. 1986. Trophic relationships in freshwater pelagic ecosystems. Canadian Journal of Fisheries and Aquatic Science **43**:1571-1681.

Mills, E.L., D.M. Green, and A. Schiavone, Jr. 1987. Use of zooplankton size to assess the community structure of fish populations in freshwater lakes. North American Journal of Fisheries Management **7**:369-378.

Nagata, T., JY. Ha, and T. Hanazato. 2005. The predation impact of larval *Pseudorasbora parva* (Cyprinidae) on zooplankton: A mesocosm experiment. Journal of Freshwater Ecology **20**:757-763.

O'Brien, W.J., and De Noyelles, Jr. 1974. Relationship between nutrient concentration, phytoplankton density, and zooplankton density in nutrient enriched experimental ponds. Hydrobiologia **44**:105-125.

Pangle, K.L., S.D. Peacor, and O.E. Johannsson. 2007. Large nonlethal effects of an invasive invertebrate predator on zooplankton population growth rate. Ecology **88**:402-412.

Persson, L. 1987. The effects of resource availability and distribution on resource utilization in perch (*Perca fluviatilis*). Oikos **48**:148-160.

Persson, L., J. Andersson, E. Wahlstrom, and P. Eklov. 1996. Size-selective interactions in lake systems: predator gape limitations and prey growth rate and mortality. Ecology **77**:900-911.

Ślusarczyk, M. 1997. Impact of fish predation on a small-bodied cladoceran: limitation or stimulation? Hydrobiologia **342/343**:215-221.

Spencer, C.N., D.S. Potter, R.T. Bukantis, and J.A. Stanford. 1999. Impact of predation by *Mysis relicta* on zooplankton in Flathead Lake, Montana, USA. Journal of Plankton Research **21**:51-64.

Stenson, J.A.E. 1976. Significance of predator influence on composition of Bosmina sp. Populations. Limnology and Oceanography **21**:814-822.

Tessier, A.J. and N. Consolatti. 1991. Resource quantity and offspring quality in Daphnia. Ecology **72**:468-478.

Tessier, A.J., A. Young, and M. Leibold. 1992. Population dynamics and body-size selection in *Daphnia*. Limnology and Oceanography **37**:1-13.

Tew, K.S., J.D. Conroy, and D.A. Culver. 2006. Effects of lowered inorganic phosphorus fertilization rates on pond production of percid fingerlings. Aquaculture **255**:436-446.

Tollrian, R. 1995. Predator-induced morphological defenses: costs, life history shifts, and maternal effects in *Daphnia pulex*. Ecology **76**:1691-1705.

Vos, M., J.G. B. J.G. Flik, J. Vijverberg, J. Ringelberg, and W.M. Mooij. 2002. From inducible defences to population dynamics: modeling refuge use and life history changes in *Daphnia*. Oikos **99**:386-396.

Weider, L.J. and J. Pijanowska. 1993. Plasticity of Daphnia life histories in response to chemical cues from predators. Oikos **67**:385-392.

Table 1. The simultaneous effects of predation and fertilization on SFR determined with ANCOVA. Our results show that SFR decreased at the same rate with increased predation independent of fertilization rate (e.g., interaction term is non-significant).

Analysis of Covariance

	df	F	*P*
	3	3.4	0.02

Parameter Estimates

	Estimate	Std. Error	*P*
Predation	-6×10^{-4}	2.7×10^{-4}	0.03
Fertilization	-6.3×10^{-3}	2.5×10^{-3}	0.01
Fertilization*Predation	4.7×10^{-8}	2.7×10^{-4}	1

Table 2. The simultaneous effect of predation and fertilization on MAX determined by ANCOVA. Our results show that MAX decreased at the same rate independent of fertilization rate (e.g., non-significant interaction term).

Analysis of Covariance			
	df	F	*P*
	3	4.9	0.00

Parameter Estimates			
	Estimate	Std. Error	*P*
Predation	-9.7×10^{-4}	1.1×10^{-2}	0.00
Fertilization	-7.1×10^{-3}	2.8×10^{-3}	0.01
Fertilization*Predation	-1.3×10^{-4}	3.1×10^{-4}	0.68

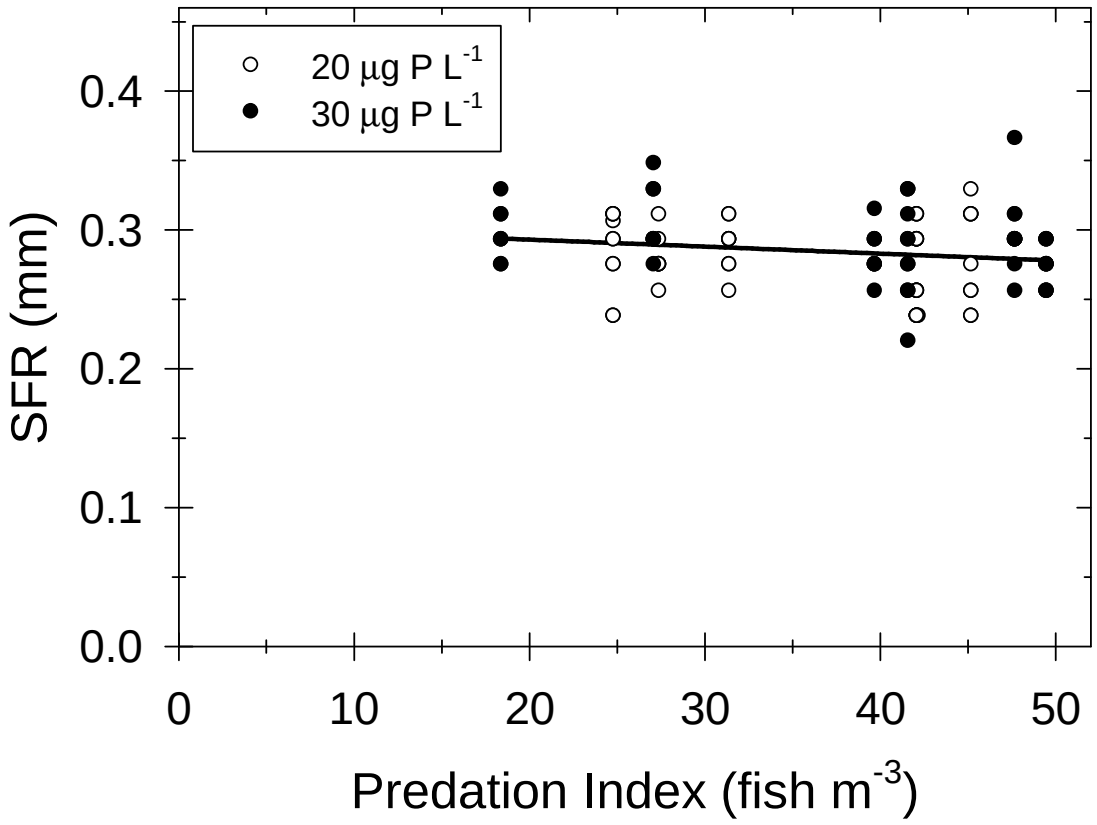

Figure 1A. The relationship between predation and SFR in ponds with different fertilization regimens. The non-filled circle data points represent ponds fertilized to 20 μg P L^{-1} and filled circles represent ponds fertilized with 30 μg P L^{-1}. The relationship between *Bosmina* SFR and fish predation is marginally significant ($F_{1,108}$ = 3.67, *P* = 0.058, R^2 = 3.3%; SFR (mm) = 0.303-0.000504 Pred. Index (m^{-3})). As predation increases, SFR decreases. This graph further compares the SFR versus predation between different levels of fertilization. With predators present, the ponds with 30 μg P L^{-1} have larger SFR than ponds with 20 μg P L^{-1}.

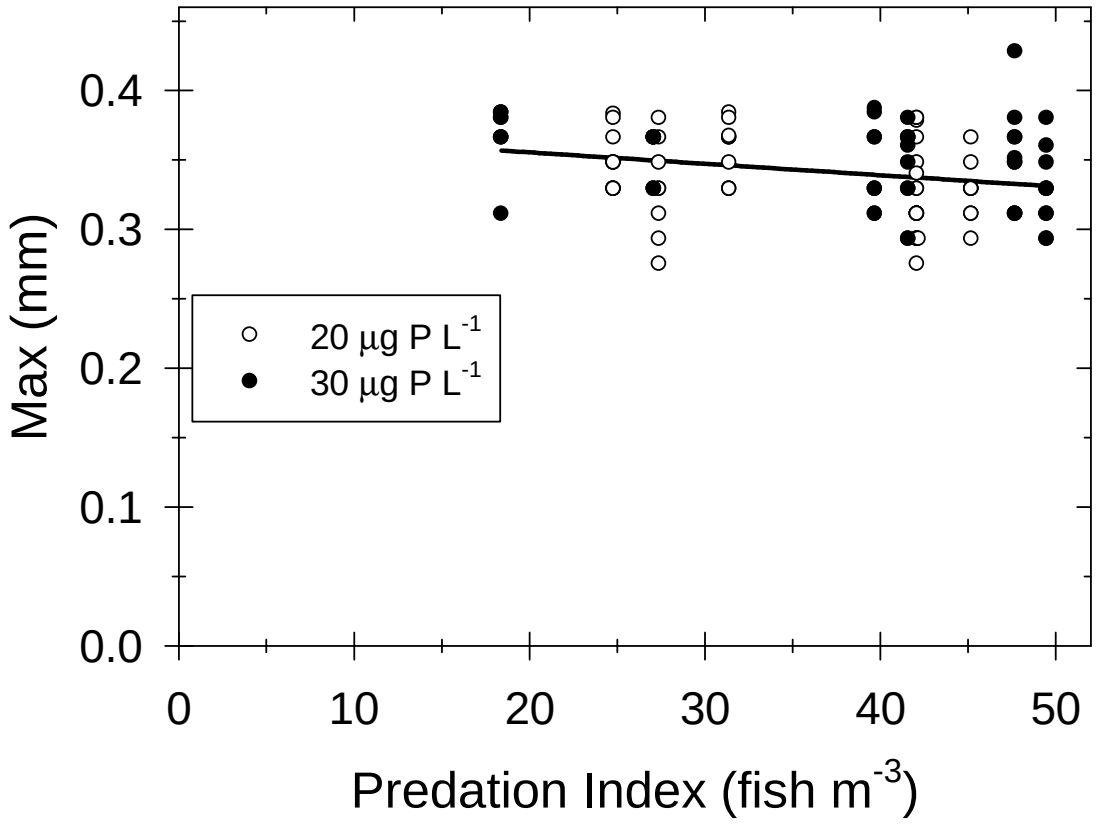

Figure 1B. The relationship between predation and MAX in ponds with different fertilization regimens. The non-filled circle data points represent ponds fertilized with 20 µg P L^{-1} and filled circles represent ponds fertilized with 30 µg P L^{-1}. Our results showed a significant decrease in MAX with an increase in predation ($F_{1,108}$ = 7.85, *P* = 0.006, R^2 = 6.8%; MAX (mm) = 0.372-000822 Pred. Index (m^{-3})).

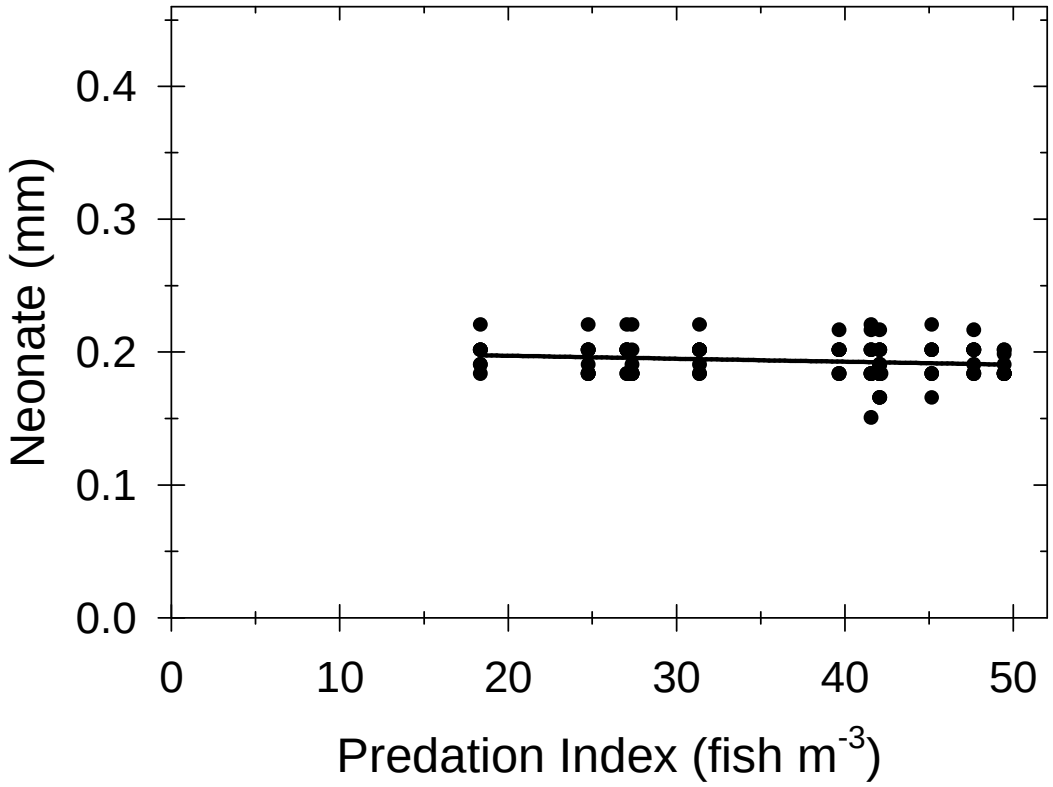

Figure 1C. The relationship between predation and NEO. NEO did not increase with predation ($F_{1,108} = 2.96$, $P = 0.088$, $R^2 = 2.7\%$; NEO (mm) = 0.202-0.000224 Pred. Index (m^{-3})). NEO did not steadily decrease, but exhibited a minimum threshold. This graph displays neonate size decreasing from a maximum of 0.22 mm to a minimum size of 0.18 mm.

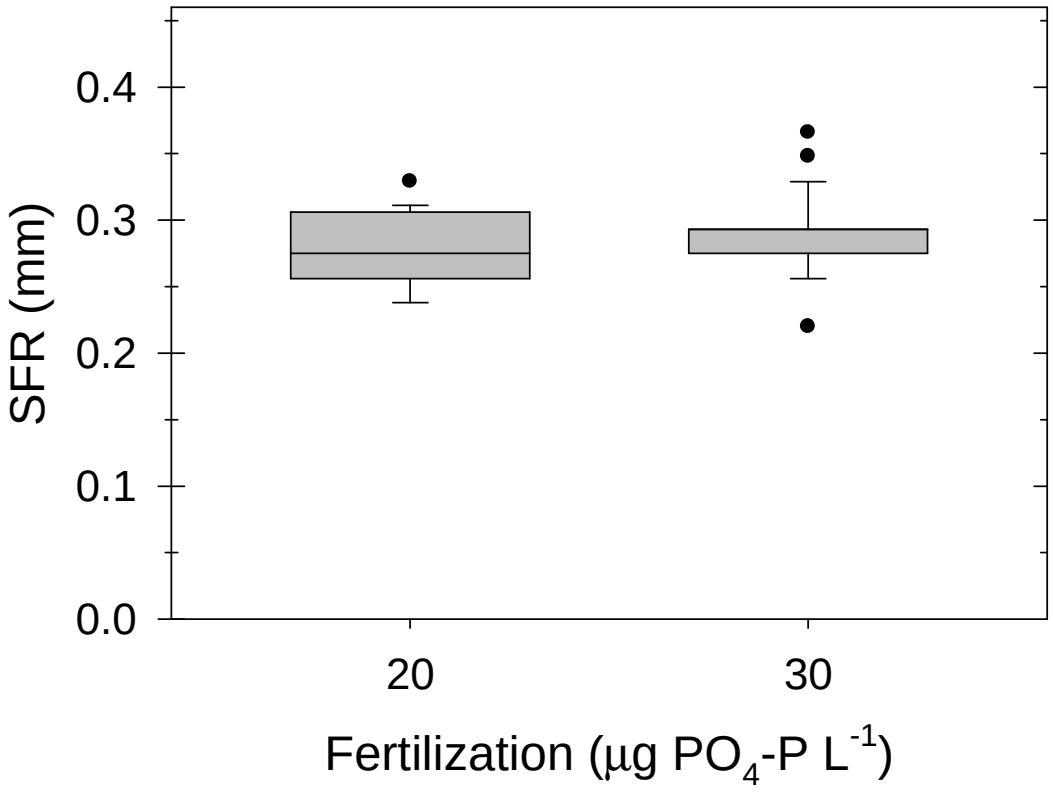

Figure 2A. The relationship between fertilization (bottom-up, nutrient effect) and SFR. Ponds were fertilized with either 20 µg P L^{-1} (represented in the graph by the 20) or 30 µg P L^{-1} (represented in the graph by the 30). SFR was significantly larger in the 30 µg P L^{-1} (one-way ANOVA, $P = 0.033$).

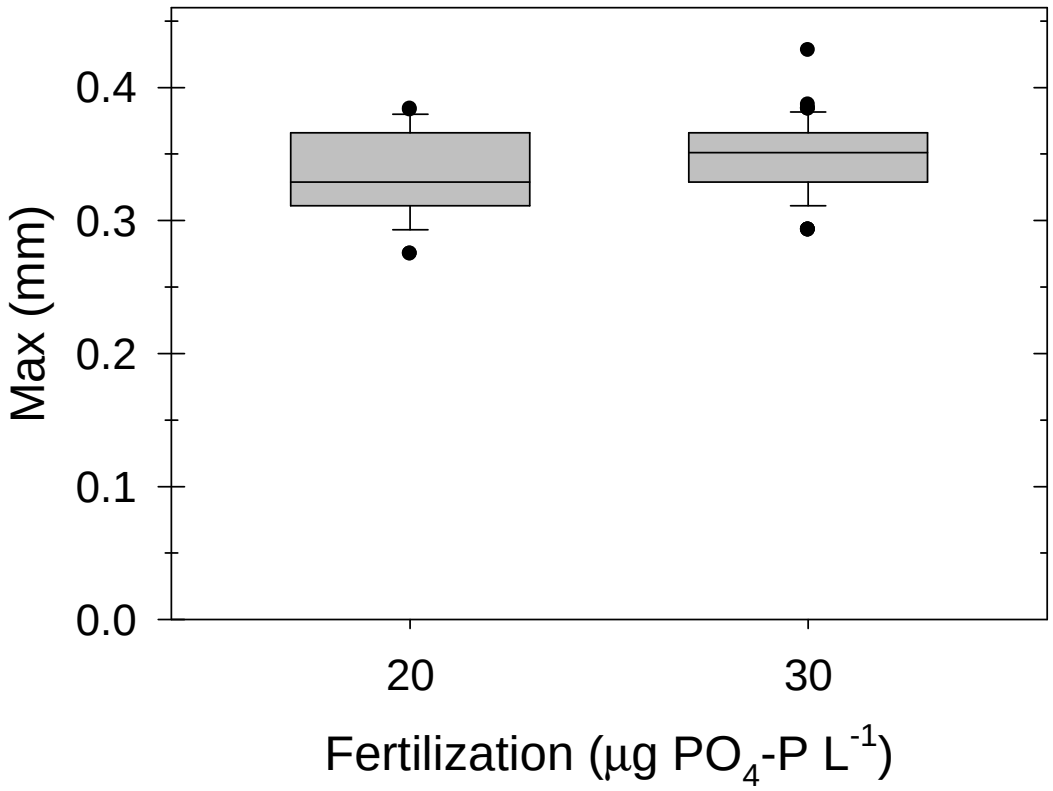

Figure 2B. The relationship between fertilization (bottom-up, nutrient effect) and MAX. Ponds fertilized at 30 µg P L^{-1} exhibited a significantly greater MAX (one-way ANOVA, $F_{1,108} = 3.84$, $P = 0.053$).

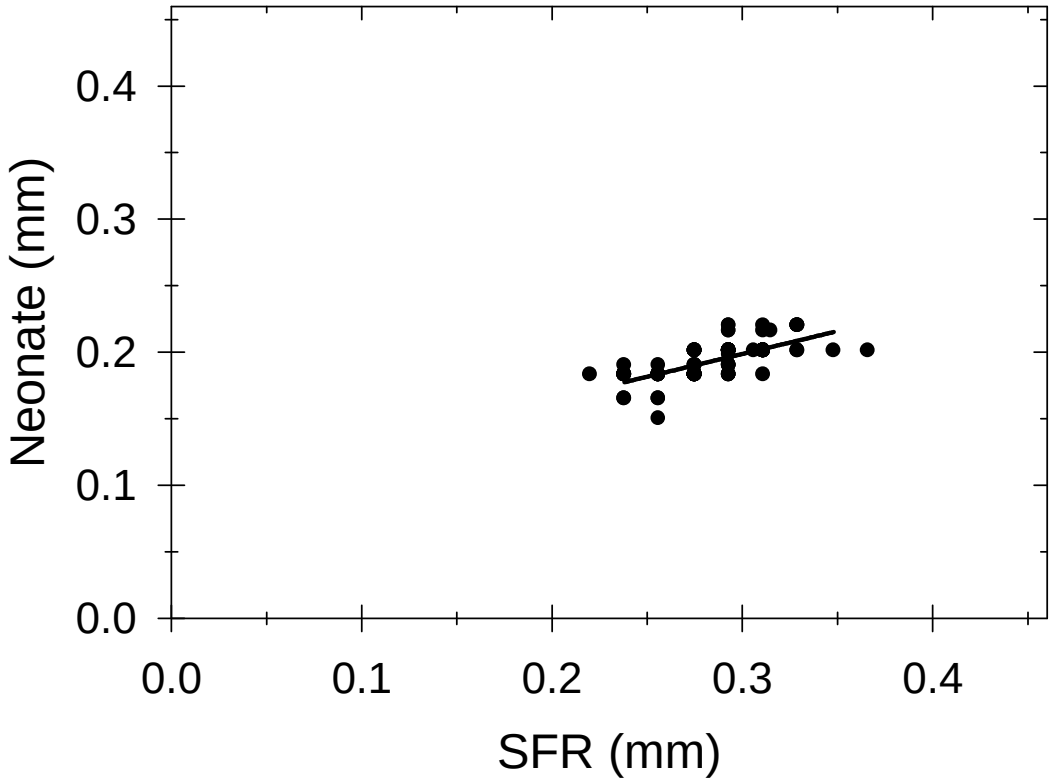

Figure 3A. The relationship between NEO and SFR showing significant correlation between life history traits ($P < 0.001$, $R^2 = 48.4\%$; NEO (mm) = 0.0958 + 0.343 SFR (mm)).

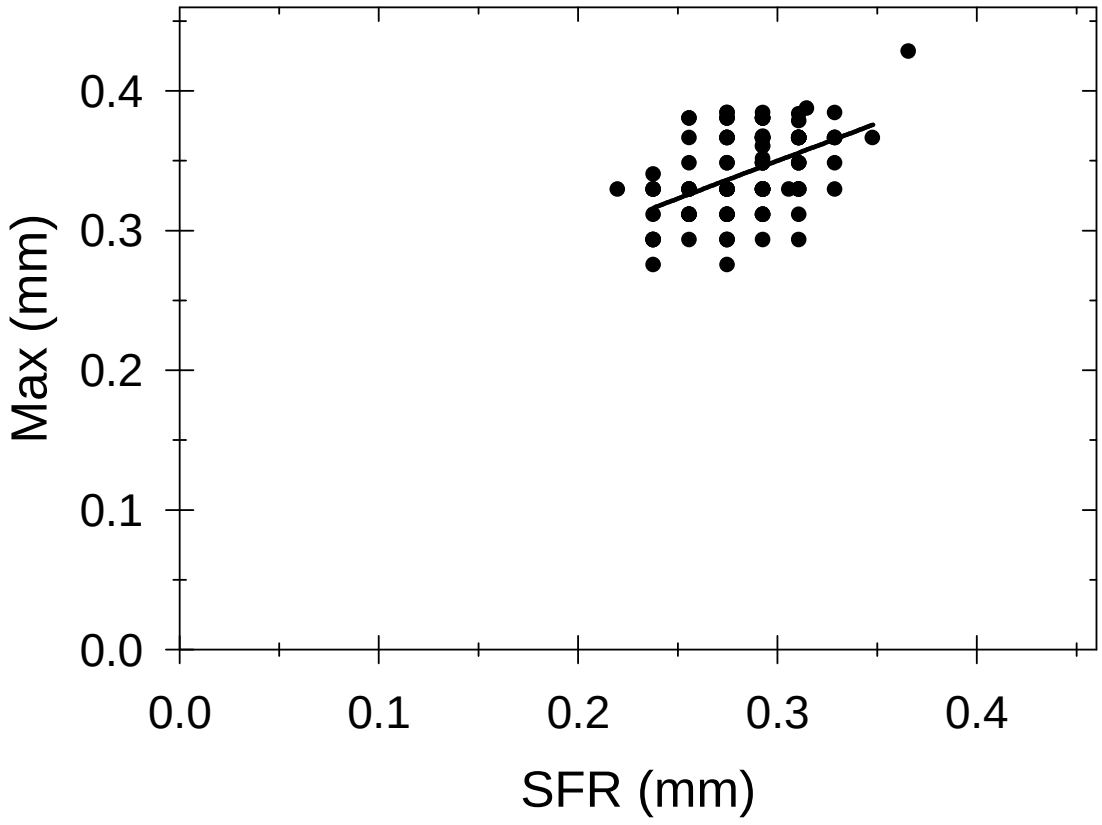

Figure 3B. The relationship between MAX and SFR showing a significant correlation between life history traits ($P < 0.001$, $R^2 = 22.6\%$; MAX (mm) = 0.188 + 0.540 SFR (mm)).

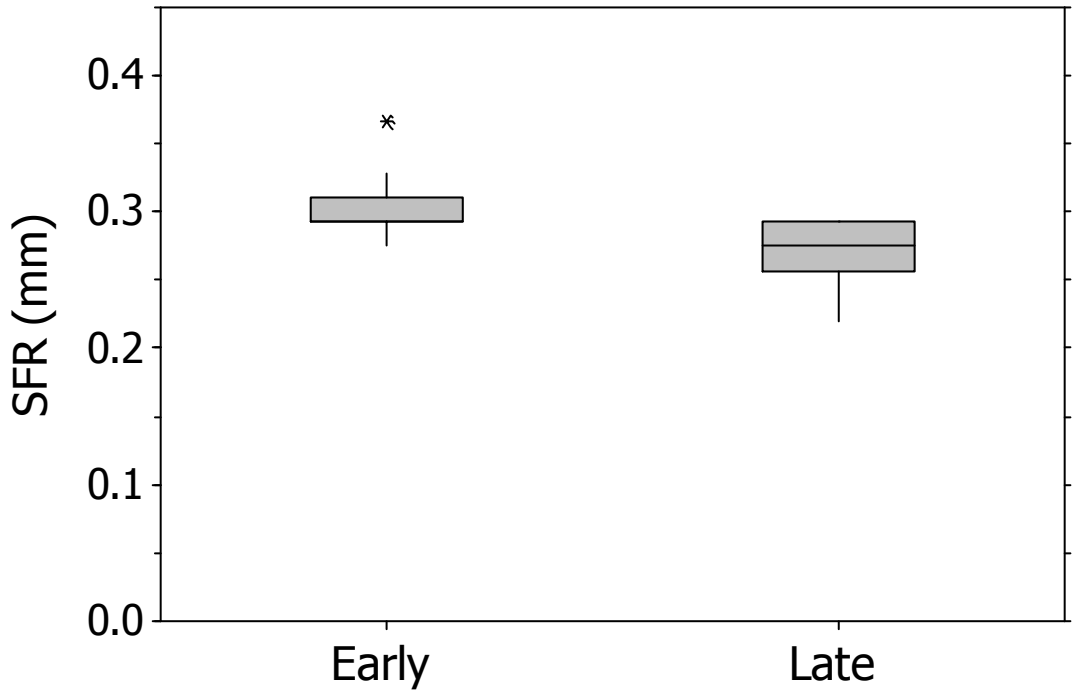

Figure 4A. The relationship between SFR and time. The first three dates of sampling represent the early time and the last three dates of sampling represent the late time. Through time, size of first reproduction decreased significantly (one-way ANOVA, $F_{1,108} = 44.86$, $P < 0.001$). Vertical lines show one standard deviation and the asterisk represents an outlier.

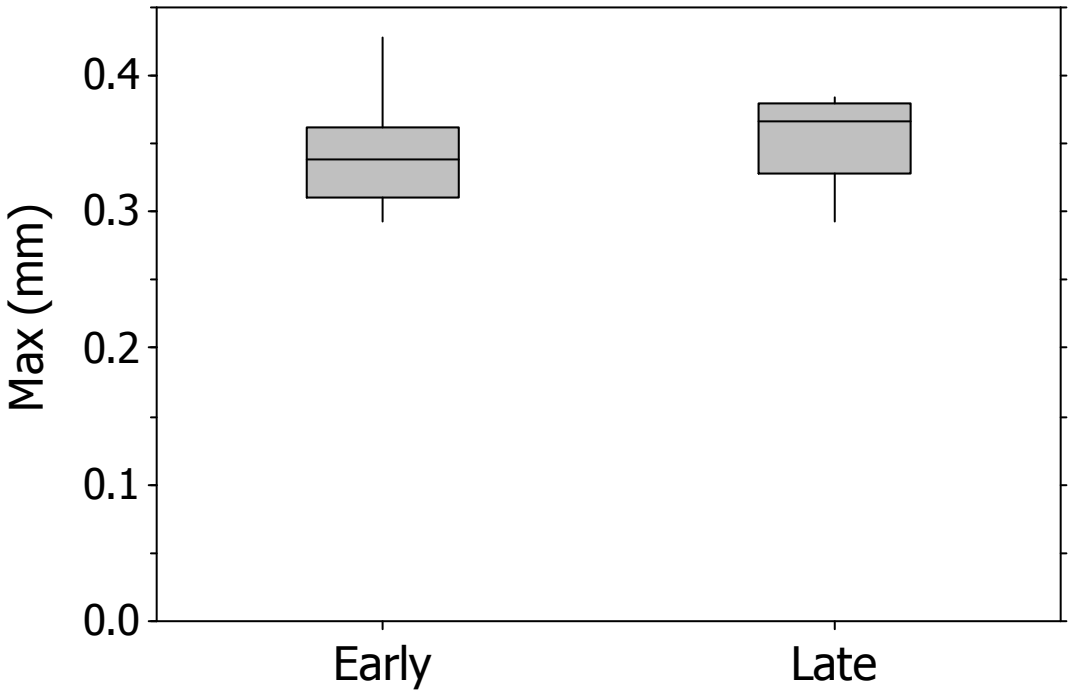

Figure 4B. The relationship between MAX and time. The first three dates of sampling represent the early time and the last three dates of sampling represent the late time. Vertical lines show one standard deviation. Contrary to our hypothesis of expecting to see MAX decrease later in the season due to a decreased in SFR, MAX significantly increased (one-way ANOVA, $F_{1,108} = 4.72$, $P = 0.034$).